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# Retrieval Orientation and the Control of Recollection: An fMRI Study

Alexa M. Morcom<sup>1</sup> and Michael D. Rugg<sup>2</sup>

## Abstract

■ This study used event-related fMRI to examine the impact of the adoption of different retrieval orientations on the neural correlates of recollection. In each of two study–test blocks, participants encoded a mixed list of words and pictures and then performed a recognition memory task with words as the test items. In one block, the requirement was to respond positively to test items corresponding to studied words and to reject both new items and items corresponding to the studied pictures. In the other block, positive responses were made to test items corresponding to pictures, and items corresponding to words were classified along with the new items. On the basis of previous ERP findings, we predicted that in the word task, recollection-related effects would be found for target information only. This

prediction was fulfilled. In both tasks, targets elicited the characteristic pattern of recollection-related activity. By contrast, nontargets elicited this pattern in the picture task, but not in the word task. Importantly, the left angular gyrus was among the regions demonstrating this dissociation of nontarget recollection effects according to retrieval orientation. The findings for the angular gyrus parallel prior findings for the “left-parietal” ERP old/new effect and add to the evidence that the effect reflects recollection-related neural activity originating in left ventral parietal cortex. Thus, the results converge with the previous ERP findings to suggest that the processing of retrieval cues can be constrained to prevent the retrieval of goal-irrelevant information. ■

## INTRODUCTION

Episodic memory retrieval occurs when a retrieval cue overlaps sufficiently with a stored memory representation to lead to the reactivation (reinstatement) of the encoded information (Morris, Bransford, & Franks, 1977; Tulving & Thomson, 1973; Tulving & Osler, 1968; see Rugg, Johnson, Park, & Uncapher, 2008). A long-standing principle of memory holds that the likelihood of retrieval success varies with the amount of overlap between the processing engaged by an episode when it was initially experienced and the processing later engaged by a retrieval cue: The greater the overlap, the greater the likelihood of retrieval (Morris et al., 1977; Tulving & Thomson, 1973; see Goh & Lu, 2012; Nairne, 2002, for caveats). Thus, the ability to adjust cue processing so as to maximize study–test overlap would permit a cue to be optimally employed to meet different retrieval goals (Jacoby, Shimizu, Daniels, & Rhodes, 2005; Robb & Rugg, 2002). The engagement of such a goal-directed cue-processing strategy is termed a retrieval orientation (Rugg & Wilding, 2000).

There is both behavioral and electrophysiological evidence that people can maintain distinct retrieval orientations. In a series of studies from our laboratory (Johnson & Rugg, 2006; Hornberger, Morcom, & Rugg, 2004; Morcom & Rugg, 2004; Herron & Rugg, 2003a; Robb & Rugg, 2002), ERPs elicited by physically identical un-

studied recognition memory test items (typically, words) were contrasted according to the nature of the to-be-retrieved information. For example, in Robb and Rugg (2002), participants undertook separate study–test cycles in which the studied items were either words or pictures and the test items were always words. ERPs elicited by unstudied test items were markedly more negative-going when pictures rather than words were the targeted material, an effect that could be dissociated from differences in the difficulty of the two retrieval tests. This finding was replicated in several subsequent studies (Hornberger, Rugg, & Henson, 2006b; Hornberger et al., 2004; Herron & Rugg, 2003a; see also Stenberg, Johansson, & Rosen, 2006).

In a complementary behavioral approach, Jacoby and colleagues (Jacoby et al., 2005) presented blocks of study items that required either “deep” or “shallow” study processing, each block being immediately followed by a recognition memory test. When recognition memory was later assessed for the unstudied items presented in each initial memory test, it was found to be more accurate for items that had been intermixed with studied items from the deep rather than the shallow study block. Jacoby and colleagues interpreted this finding as evidence for the adoption of different cue-processing strategies when performing the recognition memory test associated with each block so as to maximize overlap between study and test processing. Together, the ERP and behavioral findings provide evidence for the ability of rememberers to adjust cue-processing strategies so as to optimize study–test overlap.

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Importantly, in addition to maximizing the likelihood of successful retrieval of goal-relevant memories, the adoption of a retrieval orientation can also reduce the likelihood of retrieving irrelevant information. In the terminology of Jacoby, Kelley, and McElree (1999), retrieval cue processing can act as a “filter,” limiting the need to deploy processing resources in service of post-retrieval monitoring and evaluation, and increasing the efficiency with which memory can serve current behavioral goals. The findings of an ERP study by Herron and Rugg (2003a; see also Herron & Wilding, 2005; Herron & Rugg, 2003b) provide support for this proposal. The authors employed study lists that comprised a mixture of words and pictures, each followed by test phases in which all items were words. Following one study phase, the requirement was to make a positive recognition judgment to studied words but to classify words corresponding to studied pictures as new (along with test words corresponding to unstudied words or pictures). In a separate block, the response contingencies were reversed, such that test items corresponding to studied pictures were to be classified as “old,” and all other items endorsed “new.” In this latter condition, ERPs elicited by test items corresponding either to “target” items (studied pictures) or to “nontargets” (studied words) demonstrated the characteristic “old/new” effects that have been extensively researched for the past two decades (for a review, see Rugg & Curran, 2007). Pre-eminent among these effects was a robust “left parietal” old/new effect, widely held to be a neural signature of successful episodic recollection (Rugg & Curran, 2007; Curran, 2000; Rugg et al., 1998). In striking contrast, when words were the targeted material, only the ERPs elicited by test items endorsed as old (i.e., items corresponding to studied words) demonstrated old/new effects; the ERPs elicited by items corresponding to studied pictures were statistically indistinguishable from those elicited by unstudied (new) items. These findings were replicated by Johnson and Rugg (2006).

Herron and Rugg (2003a) interpreted their findings as evidence that, in some circumstances at least, a retrieval orientation does indeed serve to focus retrieval processing on goal-relevant memory representations. By this argument, when words were the targeted material, participants were able to process the retrieval cues in a manner that led to minimal overlap with the processing accorded pictures during the study phase, hence avoided retrieving the pictures. By contrast, the cue-processing strategy engaged when pictures were targeted was less constrained and failed to prevent the concurrent retrieval of studied words. These findings converge with those of other ERP studies that also demonstrate that retrieval cue processing can vary according to the specificity of the sought-for information (Johnson, Kounios, & Nolde, 1997; see also Ranganath & Paller, 1999) or the nature of the encoding operations (Dzulkifli & Wilding, 2005; Dzulkifli, Sharpe, & Wilding, 2004).

This study is an extension of Herron and Rugg (2003a), using the same task but with fMRI as a measure of retrieval-

related neural activity rather than ERPs. The study had two primary aims, both relating to the consequences of how retrieval cues are processed. The first aim was to obtain convergent evidence that adoption of a retrieval orientation can “gate” the retrieval of goal-irrelevant information, preventing its recollection. If Herron and Rugg’s interpretation of their ERP findings is correct, retrieval-related activity in the network of regions reported in numerous previous fMRI studies to be engaged during successful episodic memory retrieval (notably, inferior lateral parietal cortex and the posterior cingulate; see Kim, 2011; Vilberg & Rugg, 2008b, for reviews) should be equivalent in magnitude when elicited by test items corresponding to either class of targeted material. Crucially though, when pictures are targeted, test items corresponding to nontargets (studied words) should elicit retrieval success effects in recollection-sensitive regions, whereas when words are targeted, nontargets (studied pictures) should elicit diminished effects. In addition to performing a whole-brain analysis, we tested this hypothesis by assessing retrieval-related activity in a region of the left angular gyrus defined *a priori* on the basis of coordinates associated with recollection-specific activity in an earlier meta-analysis (Vilberg & Rugg, 2008b). The same ROI was also the focus of the second aim of this study, which was to further test the hypothesis that the left parietal old/new ERP effect is a direct reflection of retrieval-related neural activity in left inferior lateral parietal cortex, specifically, BA 39 in the vicinity of the angular gyrus (Vilberg & Rugg, 2008a). Evidence in favor of this hypothesis currently includes the findings that both effects are selectively associated with retrieval of qualitative information about a prior episode (recollection), rather than with recognition memory based on an *acontextual* sense of familiarity (Vilberg & Rugg, 2008b; Rugg & Curran, 2007) and that the magnitude of both ERP and fMRI effects covaries with the amount of information recollected (Vilberg & Rugg, 2007). The present experiment afforded the opportunity to test for another functional parallel: On the basis of the ERP findings described above (Johnson & Rugg, 2006; Herron & Rugg, 2003a), it was predicted that, when words are the target material, retrieval-related activity in left inferior parietal cortex elicited by items corresponding to nontargets will be attenuated relative to the activity elicited by items corresponding both to targets and to nontargets when pictures are the target material (see Herron & Wilding, 2005, for a similar line of argument). Following Herron and Rugg (2003a), we also predicted that the processing of retrieval cues would differ according to task in the absence of successful retrieval, leading to differences in the activity elicited by correctly rejected unstudied (new) items in each task.

A final aim of the current study stems from a puzzling aspect of the findings of Johnson and Rugg (2006) and Herron and Rugg (2003a). In both of these studies, the ERPs elicited by nontargets when words were the target material were statistically indistinguishable from the ERPs elicited by new items, yet the RTs to the nontarget items

were slower than the RTs to new items. Thus, items corresponding to nontargets must have engaged some kind of retrieval process, albeit not one reflected in concurrently recorded ERPs. This finding suggests that any filtering that occurred when words were the target material was incomplete. The present experiment provides the opportunity to ask whether, using fMRI, it is possible to identify differences in the neural activity elicited by nontarget and new items that shed light on the mechanisms underlying the relative slowing of responses to nontargets.

## METHODS

### Participants

Eighteen right-handed volunteers (five men) gave written consent to participate in the study. They were aged 18–34 years and reported good health, with no history of significant neurological or systemic illness. The study was approved by the University College London/UCL Hospital (ref.: 99/0048) and National Hospital/Institute of Neurology (ref.: 00/N031) Research Ethics Committees.

### Materials

The experimental stimuli and counterbalancing procedures were identical to those of Herron and Rugg (2003a). Stimuli were selected from pools of 240 words (ranging in length between four and nine letters), which were the names of 240 corresponding color pictures of objects (see Herron & Rugg, 2003a). Stimuli were divided into six pairs of corresponding picture/word lists. Each 80-item study list was formed by randomly intermixing one word list and one noncorresponding picture list. Each test list was composed of a random ordering of 40 words corresponding to the studied pictures, 40 studied words, 40 words that referred to items not studied either as pictures or words, and 40 fixation-only trials (see Procedure). Across participants, lists were rotated so that objects served equally often as studied pictures, studied words, and new items. Administration of the six study–test blocks was counterbalanced so that every studied item also served equally often as a “target” and a “nontarget” (see below). An additional nine stimuli were used to form practice lists, with a further eight stimuli serving as fillers (two at the start of each study or test phase).

### Procedure

#### *Behavioral Task*

The procedure was based on that of the ERP study of Herron and Rugg (2003a), adapted for fMRI. Practice study–test blocks were given outside the scanner, using instructions identical to those in the prior study. Two study–test blocks were then administered in the MRI scanner. In one, items studied as pictures were designated as targets (“picture task”), and in the other, items

studied as words were designated as targets (“word task”). An interval of about 1 min separated the study and test phases, during which participants were reminded of the test phase procedure. Before the appearance of the first item in each list the phrase “GET READY” appeared. At both study and test, the experimental stimuli and the fixation character “+” were presented in central vision, within a white frame subtending a visual angle of approximately  $3^\circ \times 3^\circ$ . Stimuli were presented against a gray background. Words were presented in black upper case “Arial” font letters. The order of the designated target material in the two test phases and the response hands for “old” and “new” responses were counterbalanced across subjects. Key press responses were made with the index fingers using a button box.

During the study phases, participants performed one of two tasks according to whether the stimulus presented was a picture or a word. If it was a picture, participants were asked to respond using one button if the object depicted would fit inside a shoebox, and another button if it would not. If the stimulus was a word, a pleasant/unpleasant judgment was required, using the same two response buttons. On each study trial, the fixation character was presented for 500 msec, followed by the stimulus for 1500 msec. The screen was then blanked for 200 msec, and the fixation character re-presented for a total SOA of 3000 msec.

At test, participants were asked to press one key if a word had been presented in the immediately preceding study phase in the target material (i.e., as a picture or word depending on the study–test block) and to press another key if the word was either new or had been studied in the nontarget material. On each test trial, the fixation character was first presented for 1200 msec. This was followed by a 500-msec test item presentation and then the re-presentation of the fixation character, to give a total trial length of 3120 msec. The interspersed “fixation-only” trials also lasted for 3120 msec, so the SOA varied in multiples of 3120 msec. Instructions were to respond as quickly as possible without sacrificing accuracy.

#### *fMRI Data Acquisition*

A 3-T Allegra system (Siemens, Erlangen, Germany) was used to acquire 534 T2\*-weighted transverse EPIs ( $64 \times 64 \times 3 \text{ mm}^2$  pixels, echo time = 50 msec), with BOLD contrast. EPIs comprised 30 2.5-mm-thick axial slices taken every 3.75 mm (1.25 mm gap), acquired sequentially in a descending direction with a repetition time of 1.95 sec. This gave coverage of the majority of the cerebrum but excluded the cerebellum and temporal poles. Two sessions of 267 scans were acquired, the first five volumes being discarded to allow for T1 equilibration effects. The ratio of SOA to repetition time meant that the impulse response was sampled every 390 msec (over trials). After completion of the task and EPI data acquisition, a T1 structural scan ( $256 \times 256$  matrix,  $1 \text{ mm}^3$  voxels) was acquired.



## Behavioral Analysis

Test trials with RTs greater than the trial length (3120 msec) were marked as invalid, as were no- or multiple-response trials. Trials were sorted into nine conditions of interest: (1) items studied as pictures and correctly identified as targets during picture task blocks ("picture targets"), (2) items studied as pictures and correctly classified as nontargets during word task blocks ("picture nontargets"), (3) items studied as words and correctly identified as targets during study-word blocks ("word targets"), (4) items studied as words and correctly rejected as nontargets during study-picture blocks ("word nontargets"), (5) new items correctly identified during picture task blocks ("picture task new item"), (6) new items correctly identified during word task blocks ("word task new item") and four conditions of no interest: (a) items not studied but judged to targets ("new item errors") and (b) items studied as pictures and incorrectly classified during study-picture blocks ("picture target errors"), (7) items studied as pictures but incorrectly identified as targets during word task blocks ("picture nontarget errors"), (8) items studied as words but incorrectly classified during study-word blocks ("word target errors"), (9) items studied as words but incorrectly identified as targets during study-picture blocks ("word nontarget errors").

## fMRI Analysis

Preprocessing of the fMRI data and first-level statistical modeling were performed with SPM2 ([www.fil.ion.ucl.ac.uk/spm/software/spm2/](http://www.fil.ion.ucl.ac.uk/spm/software/spm2/)). Second-level statistical modeling was performed with SPM8 ([www.fil.ion.ucl.ac.uk/spm/software/spm8/](http://www.fil.ion.ucl.ac.uk/spm/software/spm8/), r3960). All volumes were coregistered to the first volume and unwarped to allow for interactions between EPI distortions and subject movement (Andersson, Hutton, Ashburner, Turner, & Friston, 2001). The data in each slice were then interpolated in time to match the acquisition time of the middle slice. Spatial normalization was carried out using the optimized protocol in SPM2 (Ashburner & Friston, 2000). Each participant's EPI data were first coregistered with their structural scan. Normalization parameters were then estimated during segmentation of the structural scan and used to reslice the EPI time series to  $3 \times 3 \times 3$  mm voxels in MNI space. Finally, the EPI data were smoothed with an isotropic 8 mm FWHM Gaussian kernel.

Statistical analysis was performed using a two-level summary statistic procedure (Penny & Holmes, 2006). At the first level, sequences of delta functions at the event onset times for each condition were convolved with a canonical ("early") hemodynamic response function (HRF, Friston et al., 1998) and a delayed ("late") HRF (Henson, Andersson, & Friston, 2000), shifted 2.5 sec later in time than the canonical HRF. The resulting basis functions formed the covariates in a general linear model for each subject, with constant terms for each session. For each

condition, late HRF covariates were orthogonalized with respect to those for the early HRF using a Gram-Schmidt procedure, giving priority to the early covariate (Andrade, Paradis, Rouquette, & Poline, 1999). Common variance was thus attributed to the early covariate. The inclusion of the late covariate enables the detection of activity peaking later than the peak of the canonical HRF, as may sometimes occur in regions engaged in episodic retrieval (e.g., Woodruff, Uncapher, & Rugg, 2006; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997). After downsampling at the midpoint of each scan, these covariates were entered in a general linear model. Parameter estimates for each covariate were calculated from the weighted least squares fit of the model to the data, after prewhitening based on an AR(1) plus white noise model (Friston et al., 2002). The data for each session were highpass filtered to 1/128 Hz and scaled to a grand mean of 100 across all voxels and scans within a session.

Linear contrasts of first-level parameter estimates constituted the data for the second-level analyses, which treated participants as a random effect. Details of models and group-level contrasts are given in the Results (fMRI Findings: Analysis Strategy). SPMs were first thresholded at  $p < .001$ , uncorrected. To control the family-wise error (FWE) rate at  $p < .05$ , this was combined with a cluster extent threshold of 65 contiguous voxels, determined using the AlphaSim Monte Carlo simulation tool from AFNI (Analysis for Functional NeuroImaging, [afni.nimh.nih.gov/](http://afni.nimh.nih.gov/); Cox, 1996). Inclusive masks were applied at an uncorrected threshold of  $p < .001$ , and the final masked image thresholded at an FWE-corrected level using AlphaSim. To discount voxels showing any hint of exclusively masked effects, these masks were applied at an uncorrected threshold of  $p < .05$ . The locations of the peaks of suprathreshold clusters were established with reference to the subjects' structural and mean EPI images and the MNI reference brain (Cocosco, Kollokian, Kwan, & Evans, 1997). They were labeled using the systems of Talairach and Tournoux (Talairach & Tournoux, 1988) and Brodmann (Brodmann, 1909).

## RESULTS

### Behavioral Findings

Behavioral performance is summarized in Table 1. ANOVA of accuracy proportions with factors of Task, that is, Target Material (picture, word) and Item Type (target, nontarget, new) yielded reliable effects of Item Type,  $F(1.1, 19.1) = 11.56$ ,  $p < .001$ , and a Task  $\times$  Item type interaction,  $F(1.3, 22.2) = 9.81$ ,  $p < .001$ . Pairwise tests indicated that target accuracy was lower when pictures rather than words were targets,  $t(17) = -3.31$ ,  $p < .005$ , whereas nontarget accuracy was higher,  $t(17) = 2.49$ ,  $p < .05$ . Accuracy for new items did not differ reliably according to task. ANOVA of mean RTs for trials with correct responses revealed a significant interaction of Task  $\times$  Item

**Table 1.** Percent Accuracy and RT (msec) by Target Material and Item Type

Target Material	Item Type	% Correct (SD)	RT (SD)
Pictures	Targets	74 (16)	1140 (117)
	Nontargets	94 (6)	1105 (129)
	New	95 (7)	1164 (166)
Words	Targets	85 (16)	1052 (149)
	Nontargets	89 (8)	1151 (154)
	New	92 (12)	1087 (120)

type,  $F(1.6, 27.3) = 7.70, p < .005$ . Pairwise tests showed that target RTs were slower when pictures rather than words were targets,  $t(17) = 3.15, p < .01$ , as were new item RTs,  $t(17) = 2.43, p < .05$  (nontarget RTs were nonsignificantly faster when pictures were targets,  $t(17) = 1.28$ ).

Planned analyses were employed to assess whether performance for correct rejections differed according to Item Type (nontarget vs. new) or Task (picture vs. word). ANOVA did not give rise to any significant effects for accuracy, although this was slightly higher when targets were pictures than words,  $F(1, 17) = 3.20, .05 < p < .1$  (other  $F < 1$ ). For RTs, ANOVA revealed a significant interaction,  $F(1, 17) = 9.05, p < .01$  (for main effects,  $F < 1$ ). As already noted, responses to new items were faster when words were targets, and responses to nontargets were somewhat faster when pictures were targets. Importantly, in the word task, new items were correctly classified faster than nontargets were,  $t(17) = 3.45, p < .005$ ; the opposite tendency in the picture task was not reliable.

## fMRI Findings

### Analysis Strategy

The main, whole-brain fMRI data analysis focused on the effects of task—that is, whether words or pictures were the targets—on fMRI old/new effects (see Introduction) elicited by targets and nontargets. For each participant, four contrasts assessed the simple old/new effects for targets and nontargets according to the task. In each case, the contrasts compared the level of activity elicited by correctly classified target and nontarget old items and new items. These contrasts were therefore: picture target old/new effects (picture targets—new in the picture task), picture nontarget old/new effects (word nontargets—new in the picture task), word target old/new effects (word targets—new in the word task), and word nontarget old/new effects (picture nontargets—new in the word task; note that these contrasts are named according to the task and therefore the targeted material; see Methods for definition of conditions).

The group-level analysis of old/new effects was implemented in an ANOVA model of the four basic old/new

contrasts described above. This enabled tests both of main effects of old versus new across tasks and of modulations of old/new effects by task, using appropriate group-level contrasts. We tested our two principal hypotheses regarding target and nontarget old/new effects in two stages. Because these hypotheses concerned activity increases for old relative to new items, unidirectional  $T$  contrasts were employed to identify common effects of old > new, and bidirectional  $F$  contrasts were employed to identify interaction effects of Old/New  $\times$  Task. In Stage 1, we asked which regions showed common effects of old > new in both picture and word tasks. For targets and nontargets, the picture task old > new effect was inclusively masked with the word task old > new effect, and the resultant effects were exclusively masked with the relevant interaction between task and old versus new (i.e., for targets or nontargets, the interaction of Old/New  $\times$  Task; see Methods).

In Stage 2, we asked which regions showed old/new effects that differed according to task; that is, we identified regions demonstrating an interaction between Old/New  $\times$  Task, separately for targets and for nontargets. At each stage, bidirectional ( $F$ ) contrasts were computed and thresholded at a whole-brain corrected level (see Methods: fMRI Analysis). Plots of parameter estimates were then used to explore the data, and where relevant, post hoc  $T$  contrasts were used to determine the reliability of key simple effects. To test our third hypothesis, that old/new effects would be evident for nontargets in the word task, a separate analysis was also conducted to examine old/new effects specifically for nontargets in the word task. As this analysis was exploratory with regard to direction of old/new effects, a bidirectional  $F$  contrast was used.

In addition to the whole-brain analyses, old/new effects were also assessed in a left lateral parietal ROI defined a priori. This was centered on the coordinates closest to the peak of the center of mass of the left parietal recollection-specific old/new effects identified in the meta-analysis of Vilberg and Rugg (2008b). The peak was localized to the left angular gyrus ( $x = -43, y = -66, z = 38$ ). The ROI was defined as a 5-mm-radius sphere centered on the voxel closest to the peak of the a priori coordinates. An ANOVA was conducted on the extracted mean old > new parameter estimates for targets and for nontargets, with task as the second factor. The significance level was set at .05 for these hypothesis-driven tests.

Finally, we searched for differences in the activity elicited by correctly rejected new items in the two tasks. We employed both a whole brain and an ROI approach. The whole-brain analysis used a bidirectional ( $F$ ) contrast, thresholded at the whole-brain FWE-corrected level. We also contrasted new item activity in a set of ROIs that were derived from the peak coordinates of clusters reported in two previous studies that investigated new item retrieval orientation effects (Hornberger, Rugg, & Henson, 2006a; Woodruff et al., 2006). ROIs were defined as 5-mm-radius spheres centered on the voxels closest to the peaks of

each coordinate. Bidirectional one-sample  $t$  tests were conducted on the parameter estimates from these ROIs for the new items from the word and the picture tasks. Details of the coordinates and the contrasts employed in the original studies are given in Supplementary Table 1.

### Common Effects of Old/New

Regions in which old items elicited greater activity than new items for targets and, separately, for nontargets, independent of task, are illustrated in Figure 1 and listed in Table 2. For nontargets, robust effects were apparent bilaterally in superior lateral parietal cortex and the intraparietal sulcus, regions consistently identified in previous event-related fMRI studies of successful retrieval (for a review see Kim, 2011; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Vilberg & Rugg, 2008b; Skinner & Fernandes, 2007; Wagner, Shannon, Kahn, & Buckner, 2005). For targets, additional effects were evident in left inferior frontal gyrus, left middle temporal gyrus, right middle temporal gyrus, precuneus and posterior cingulate, and, importantly, in the left inferior parietal lobule in the vicinity of the angular gyrus (BA 39; Figure 1 and Table 2).

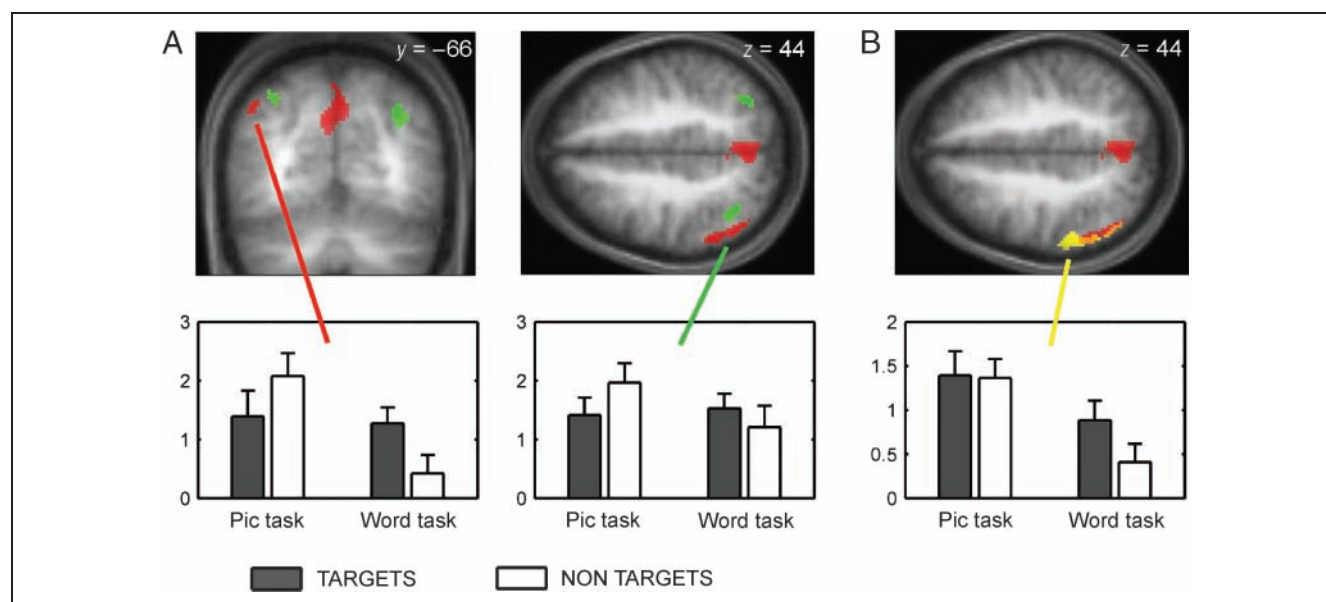
### Differential Old/New Effects According to Task

Regions in which the magnitude of old/new effects varied according to task are illustrated in Figures 1 and 2 and

listed in Table 3. For targets, no regions demonstrated a reliable old/new by task interaction. For nontargets, however, there were differential old/new effects in several regions, including the left inferior parietal lobule (BA 39), precuneus, posterior cingulate, and medial pFC. Directional post hoc analyses indicated that in all cases these interactions reflected larger old/new effects for nontargets in the picture than in the word task (see also Figures 1 and 2). Follow-up  $T$  contrasts assessed the simple effects of old/new for nontargets in the two tasks separately. The outcomes of these tests are listed in Table 3. In all of the regions showing differential nontarget old/new effects, old > new effects were reliably present for nontargets in the picture task, with evidence of word nontarget old/new effects only at a reduced threshold. In addition, reversed (new > old) effects were reliable for nontargets in the word task in medial pFC, particularly in a sub-genual region (see Table 3).

### Nontarget Old/New Effects in the Word Task

A planned contrast revealed that, in the word task, greater activity was elicited for nontargets than for new items in right lateral parietal cortex (BA 39;  $x = 36$ ;  $y = -64$ ;  $z = 38$ ; peak  $Z = 3.67$ , 75 voxels) and the posterior portion of the left inferior frontal gyrus (BA 44/BA 47;  $x = -28$ ,  $y = 26$ ,  $z = 0$ ; peak  $Z = 3.83$ , 79 voxels; see Figure 2), in the vicinity of the frontal operculum. Both of these regions had shown common



**Figure 1.** Parietal old/new effects. (A) Nontargets: Common effect of old/new (green) and interaction of Old/New  $\times$  Task (red). (B) Recall-related: Common effect of old/new for targets (yellow) and interaction of Old/New  $\times$  Task (red). Sections show the effects displayed on the group average structural image at the thresholds used for the analyses. In B, voxels also showing common effects of old/new for nontargets have been removed from the target common effects for display purposes, using exclusive masking at  $p < .05$ , uncorrected. Parameter estimate plots show target and nontarget old/new effects at the principal left parietal peaks for the indicated clusters: nontarget common effect ( $x = -40$ ,  $y = -58$ ,  $z = 48$ ), Nontarget  $\times$  Task interaction ( $x = -48$ ,  $y = -66$ ,  $z = 44$ ), and target common effect ( $x = -58$ ,  $y = -52$ ,  $z = 40$ ). Y axes show parameter estimates for old/new; arbitrary units. See Methods and Analysis Strategy for details of contrasts and clusters.

**Table 2.** Common Effects of Old/New across Picture and Word Tasks

<i>Location of Peak (x, y, z)</i>	<i>n in Cluster</i>	<i>Region</i>	<i>Brodmann's Area</i>
<i>Common Old/New Effects for Targets: Old &gt; New</i>			
−58 −52 40	1040	Left inferior parietal lobule	BA 40
		This cluster encompasses subpeaks:	
−56 −40 44		Left inferior parietal lobule	BA 40
−60 −54 32		Left supramarginal gyrus	BA 40
−34 22 −10	520	Left inferior frontal gyrus (operculum)	BA 47
32 −70 46	1230	Right superior parietal lobule	BA 7
		This cluster encompasses subpeak:	
10 −72 44		Right precuneus	BA 7
62 −34 −14	70	Right middle temporal gyrus	BA 21
−60 −52 −10	106	Left inferior temporal gyrus	BA 37
	90	Cingulate gyrus	BA 23
<i>Common Old/New Effects for Nontargets: Old &gt; New</i>			
−40 −58 48	76	Left superior parietal lobule/inferior parietal sulcus	BA 7
30 −72 44	131	Right superior parietal lobule/inferior parietal sulcus	BA 7

Regions tabulated show significant ( $p < .001$ , cluster size  $> 65$ ) main effects of old  $>$  new, using unidirectional ( $T$ ) tests. For targets and for nontargets, the picture task old  $>$  new effect was inclusively masked with the word task old  $>$  new effect and the relevant interaction of target material  $\times$  old versus new then discounted using exclusive masking (see Methods and Analysis Strategy).  $Z$  statistics are not given for these inclusively masked contrasts.  $n$  refers to the number of voxels in each cluster, and  $x$ ,  $y$  and  $z$  refer to distances in millimeters from the origin in MNI space (see Methods).

old  $>$  new effects for targets, but not for nontargets, at the strict threshold used in the original analyses. However, plots of parameter estimates suggested that old  $>$  new effects were also evident for picture as well as word task nontargets. To confirm this, post hoc  $t$  tests were conducted on the parameter estimates from each region, averaged across task. In both regions, target and nontarget old  $>$  new effects were reliable ( $p < .005$ ).

#### *Left Parietal ROI*

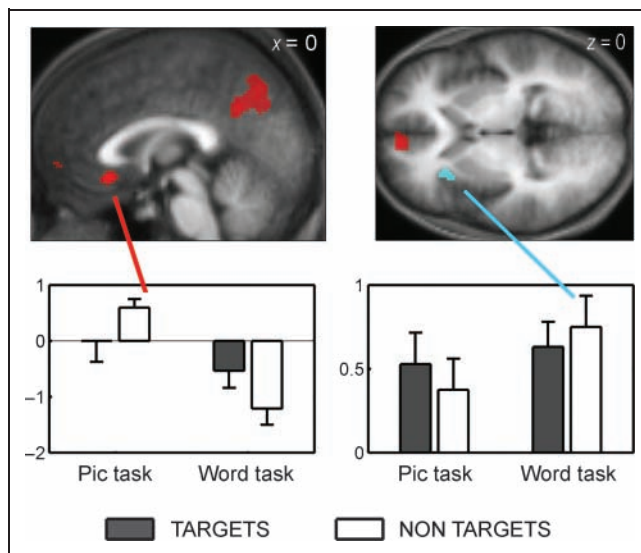
The results of the ROI analysis for the left angular gyrus are shown in Figure 3. ANOVA of the old/new effects had factors of Task (picture, word) and Target/Nontarget Status (target, nontarget). This revealed a significant main effect of Task and an interaction of Task and Target/Nontarget Status,  $F(1, 17) = 6.43$ ,  $p < .05$ ;  $F(1, 17) = 4.64$ ,  $p < .05$ , respectively. The effects reflected the fact that old/new effects in this region were substantial in the picture task for both targets and nontargets, but in the word task were only reliable for targets. Follow-up tests further demonstrated that old/new effects differed according to task for nontargets only,  $T(17) = 3.56$ ,  $p < .005$  (for targets,

$T < 1$ ), and that target old/new effects were reliably present in both tasks [for picture task,  $T(17) = 3.39$ ,  $p < .005$ ; for word task,  $T(17) = 2.62$ ,  $p < .05$ ] whereas nontarget old/new effects were only significant in the picture task [ $T(17) = 4.88$ ,  $p < .001$ ; for word task ( $T(17) = 1.80$ ,  $ns$ ).

#### *New Item Analyses*

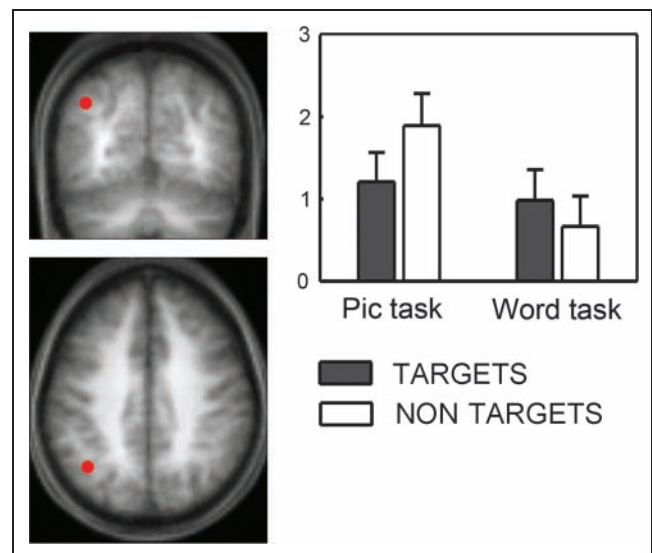
The whole-brain analysis comparing activity elicited by correctly rejected new items in the picture and word tasks revealed a single region, in right middle occipital gyrus, where activity was greater in the word than in the picture task (BA 19; 114 voxels; peak  $Z = 3.89$ ,  $x = 40$ ,  $y = -70$ ,  $z = 8$ ). The ROI analyses for new item retrieval orientation effects revealed significant results in 5 of the 13 regions previously reported to show greater activity for correct rejections when words rather than pictures were the targeted material. The present effects were evident in bilateral parietal operculum (BA 40/BA 41;  $x = -48/54$ ,  $y = -33$ ,  $z = 27$ ), left superior lateral parietal cortex (BA 7;  $x = -27$ ,  $y = -57$ ,  $z = 39$ ), left superior/middle temporal gyrus (BA 21;  $x = -60$ ,  $y = -21$ ,  $z = -3$ ), and right anterior pFC (BA 10;  $x = 45$ ,  $y = 54$ ,  $z = 0$ ;





**Figure 2.** Frontal old/new effects. Sections highlight regions showing old/new effects for word task nontargets: interactions of Old/New  $\times$  Target material (red) and simple old/new effects for word nontargets (cyan). Clusters are displayed on the group average structural image at the thresholds used for the analyses. Parameter estimate plots show target and nontarget old/new effects at the principal peaks for the indicated clusters: (left) the subgenual medial frontal interaction of Old/New  $\times$  Target material ( $x = 0, y = 28, z = -10$ ), and (in right plot) the left frontal opercular old/new effect for word nontargets ( $x = -28, y = 26, z = 0$ ). Y axes show parameter estimates for old/new; arbitrary units. See Methods and Analysis Strategy for details of contrasts and clusters.

for details of all regions and tests, see Supplementary Table 1). In all cases, activity in this study was in the same direction as was reported previously, that is, greater new item activity in the word task. There were no significant results in any of the eight ROIs previously documented



**Figure 3.** ROI analysis. The red circle indicates the position of the 5-mm-radius left angular gyrus ROI, displayed on the group average structural image ( $x = -43, y = -66, z = 38$ ). Parameter estimate plot shows old/new effects averaged across the ROI. Y axis shows parameter estimates for old/new; arbitrary units. See Methods and Analysis Strategy for details of contrasts and clusters.

to show greater activity for correct rejections when the targeted material was pictorial.

## DISCUSSION

### Behavioral Findings

The patterns of accuracy scores and RTs across tasks and response categories were similar to the patterns reported previously (Johnson & Rugg, 2006; Herron & Rugg, 2003a).

**Table 3.** Differential Nontarget Old/New Effects in Picture–Target and Word–Target Tasks

Location of Peak ( $x, y, z$ )	Peak Z	$n$ in Cluster	Region	Brodmann's area	Post hoc: Old > New	Post hoc: New > Old
<i>Picture Block Nontarget Old/New &gt; Word Block Nontarget Old/New</i>						
0 28 -10	4.43	196	Medial frontal gyrus (subgenual)	BA 11	Pic*	Word
-8 58 0	3.93	124	Medial frontal gyrus	BA 10	Pic	
-48 -66 46	4.34	169	Left inferior parietal lobule	BA 39	Pic, Word*	
			This cluster encompasses subpeak:			
-56 -48 44			Left inferior parietal lobule			
-2 -56 36	3.90	660	Bilateral precuneus	BA 31/BA 7	Pic, Word*	
18 12 54	4.12	308	Right superior frontal gyrus	BA 6	Pic	

Regions tabulated show significant ( $p < .001$ , cluster size  $> 65$ ) differential nontarget old/new effects for the picture compared with the word task using a bidirectional ( $F$ ) test. Nontarget old/new effects contrast activity for nontarget hits and correctly rejected new items. Note that the analysis of differential target old/new effects by target material block returned no significant results (see Results). Regions are listed according to the direction of the difference as revealed by post hoc comparisons (see Methods and Analysis Strategy). For further details, see legend to Table 2 and Methods.

\*Indicates post hoc tests reliable at  $p < .01$ , but not at  $p < .001$ .

Notably, accuracy was greater for the detection of word targets than picture targets, whereas the opposite was the case for nontargets. As suggested previously (Herron & Rugg, 2003a; Robb & Rugg, 2002), the greater accuracy for word targets likely reflects the beneficial effects of full versus partial overlap between the study items and retrieval cues, which more than counteracted the “picture superiority effect” that would have been observed if picture memory had been tested for using “copy cues” (Mintzer & Snodgrass, 1999; Stenberg, Radeborg, & Hedman, 1995; Madigan, 1983). The greater accuracy for picture than for word nontargets likely also reflects the benefit of study–cue overlap to some degree. However, the difference in RTs to new items (as well as the fMRI findings discussed below) suggests that differential cue overlap is not a complete account of task performance and that the bases for rejecting items differed between the two tasks. The RT effects indicate that subjects waited longer in the picture task than in the word task before judging items to be nontargets, suggesting that they adopted different retrieval strategies in the two tasks. We consider the nature of these strategies below in the light of the fMRI results. Also consistent with previous findings, RTs for nontargets in the word task were slower (by around 60 msec) than were the RTs to new items. As was noted in the Introduction, this finding indicates that whatever the beneficial effects of adopting a retrieval orientation that putatively prevented recollection of nontargets in the word task (see below), these items nonetheless engaged a retrieval process that impeded their rejection as nontargets.

### **Parietal Old/New Effects**

Relative to correctly rejected new items, target items in both conditions elicited enhanced activity in lateral parietal cortex, extending ventrally from the vicinity of the intraparietal sulcus (BA 7) into the supramarginal and angular gyri (BA 40/BA 39), consistent with numerous prior studies (see Kim, 2011; Cabeza et al., 2008; Vilberg & Rugg, 2008b; Skinner & Fernandes, 2007; Wagner et al., 2005, for reviews). A strikingly different pattern of effects was observed for nontarget items, however. Whether analyzed using a whole-brain or a ROI approach, nontarget old/new effects were evident in left ventral parietal cortex only in the picture task, that is, for nontarget items studied as words. Task-independent nontarget old/new effects were confined to more dorsal bilateral parietal regions in the vicinity of the intraparietal sulcus (and in medial parietal and frontal opercular regions identified in the planned word nontarget analysis; see below). These findings are easily accommodated by the assumption that, regardless of task, target detection was associated with successful recollection, whereas nontargets were recollected only in the picture task.

The task-dependence of nontarget old/new effects in the left angular gyrus, which were present only when pictures were targeted, was predicted on the basis of pre-

viously reported ERP results. The task-independence of the target old/new effects is also consistent with the earlier ERP findings (Johnson & Rugg, 2006; Herron & Rugg, 2003a). As outlined in the Introduction, it was reported in these prior studies that the left parietal old/new ERP effect was elicited by both word and picture targets, but by nontargets only when pictures were the target material. In light of the evidence linking the left parietal ERP effect to recollection-driven recognition memory (see Rugg & Curran, 2007), these findings were interpreted as evidence for the adoption, when words were the targets, of a retrieval orientation that prevented retrieval cues from accessing episodic memory representations corresponding to studied pictures. Like the left parietal ERP effect, retrieval-related activity in the left angular gyrus appears to be a specific neural correlate of successful recollection (Kim, 2011; Vilberg & Rugg, 2008b). Therefore, the foregoing account is equally applicable here. Together, the present and previous findings provide powerful converging evidence that the processing of retrieval cues can be biased so as to control the contents of recollection.

As already noted, the present findings suggest that whereas participants were able to prevent recollection of nontargets in the word task, this was not possible when pictures were the target material. The findings raise the question: What determines when recollection can be gated to prevent the retrieval of irrelevant information? A key factor may be the degree of overlap between the representations derived from a retrieval cue and stored memory representations (Hornberger et al., 2004; Herron & Rugg, 2003a). According to the principle of transfer appropriate processing, the greater this overlap, the more likely is it that retrieval will succeed (Morris et al., 1977). Participants can maximize the overlap between cue and memory representations by focusing the processing of a retrieval cue so as to generate a cue representation that optimally matches the targeted material (“cue bias” in the terminology of Anderson & Bjork, 1994). Similarly, it may also be possible to process a retrieval cue so as to minimize overlap with irrelevant or interfering memory representations (nontargets in the present case). As proposed by Herron and Rugg (2003a), the degree to which such overlap can be reduced may determine whether gating of recollection is possible. For example, in the present word task, the processing of test words could have focused on lexical and orthographic levels of representation, minimizing the potential for overlap with memory representations of corresponding nontarget pictures, which would largely be confined to conceptual levels of representation (Woodruff et al., 2006; Herron & Rugg, 2003a). By contrast, there is no level of representation at which the test words would not overlap with studied words, making it impossible to gate recollection by avoiding overlap between cue and nontarget memory representations when the latter correspond to words. Thus, although other factors also may operate to determine when nontarget recollection can be gated in exclusion

tasks (Mecklinger, 2010; Džulkifli & Wilding, 2005; Herron & Wilding, 2005; Džulkifli et al., 2004; Herron & Rugg, 2003b; Ranganath & Paller, 1999), we suggest that the asymmetry observed between the word and picture tasks in this study and those of Johnson and Rugg (2006) and Herron and Rugg (2003a) is attributable to the differing opportunities available in each task to minimize representational overlap between the retrieval cues and nontarget memory representations (see also Džulkifli, Herron, & Wilding, 2006; Džulkifli & Wilding, 2005; Herron & Wilding, 2005; Herron & Rugg, 2003b; Dywan, Segalowitz, & Webster, 1998).

The present findings add to the list of parallel findings for the left parietal old/new ERP effect and the fMRI old/new effects that have consistently been reported in ventral lateral parietal cortex. For example, in studies employing the “Remember/Know” procedure, both effects are only evident or are markedly greater in magnitude when recognized items are associated with the retrieval of qualitative information about the study event (Remember) than when retrieval of such information fails (Know; see Kim, 2011; Vilberg & Rugg, 2008b). Moreover, the magnitude of both the ERP and the fMRI effects covaries not merely with whether an item is recollected or not, but with the amount of information that is recollected (Guerin & Miller, 2011; Vilberg & Rugg, 2007, 2008a, 2009; Vilberg, Moosavi, & Rugg, 2006). Together with these previous findings, the present results support the proposal that the left parietal old/new ERP effect is the electrophysiological correlate of recollection-related enhancement of the fMRI BOLD signal in the angular gyrus and adjacent regions of left ventral lateral parietal cortex.

The left angular gyrus was not the only parietal region where retrieval-related activity elicited by nontarget items was modulated by target material. An extensive area of bilateral medial parietal cortex (precuneus) also demonstrated enhanced nontarget old/new effects when pictures rather than words were the target material (see Table 3 and Figure 1). Old/new effects in this region are reported as consistently as those in lateral parietal regions (see Kim, 2011; Cabeza et al., 2008; Vilberg & Rugg, 2008b; Skinner & Fernandes, 2007; Wagner et al., 2005, for reviews). Unlike the effects localized to the angular gyrus, however, these medial effects do not appear to be selectively associated with recollection-based recognition and are frequently also evident when recognition is seemingly familiarity based (Kim, 2011; Vilberg & Rugg, 2008b). Nonetheless, the nontarget old/new effects in this region, just as in the left angular gyrus, presumably reflected the retrieval orientation adopted by subjects in the target word condition.

### New Item Effects

Activity elicited by correctly identified new items differed according to task in both the whole-brain and the ROI analyses, paralleling Herron and Rugg’s (2003a) ERP find-

ings of differential new item processing in this experimental procedure (see also Woodruff et al., 2006). The ROI analyses revealed increased new item activity in the word task in areas previously reported to show enhanced new item activity when, relative to pictures, either visual (Woodruff et al., 2006) or auditory (Hornberger et al., 2006a) words were targeted. However, no regions demonstrated enhanced new item activity in the picture task. In the earlier fMRI studies, the new item effects were interpreted as reflecting material-specific cue-processing strategies leading to the generation of cue representations that maximally overlapped with targeted memory representations, for example, by focusing on the visual or phonological features of a test word when the targets were visually or auditorily studied words, respectively (Hornberger et al., 2006a; Woodruff et al., 2006; see also McDuff, Frankel, & Norman, 2009; Jacoby et al., 2005). The present findings suggest that, although subjects biased their processing of test words to enhance overlap with studied words when these were targeted, test words were not subjected to a material-specific processing strategy when pictures were the targets. The findings are therefore consistent with the proposal, outlined above, that the finding that nontarget recollection was gated only in the word task reflected the differential opportunities provided by the two tasks for modulating overlap between cue representations and target and nontarget memory representations.

### Nontarget Old/New Effects in the Word Target Condition

Although ventral and medial parietal nontarget old/new effects in the word task were much attenuated relative to those in the picture task, effects were evident in several other regions, as was anticipated given the prior behavioral evidence that it is harder in this task to reject nontargets than unstudied items (see Introduction). Old/new effects common to the two classes of nontarget item were evident in bilateral superior parietal cortex (in the vicinity of the intraparietal sulcus; see Figure 1). Additionally, an analysis restricted to the nontarget items from the word target condition identified old/new effects in the left frontal operculum. Finally, the differential nontarget old/new effect identified in ventromedial frontal cortex was driven primarily by a reversed old/new effect specific to the word task nontargets (see Table 3; Figure 2). These findings contrast with those from previous ERP studies (Herron & Rugg, 2003a; see also Herron & Rugg, 2003b), where the waveforms elicited by word task nontarget items were statistically indistinguishable from those elicited by correctly rejected new items (see Introduction). The reason for these different findings is unclear, but one obvious possibility is that fMRI is the more sensitive method for detecting certain types of retrieval-related activity. Resolution of this issue will likely have to wait until ERP and fMRI data are acquired in the same study and, ideally, concurrently.

Whatever the reason for the lack of equivalent ERP effects, the finding of reliable fMRI old/new effects for nontargets in the picture task converges with the behavioral findings to indicate that these items elicited retrieval of some kind of information. Presumably, the detection and subsequent discounting of this retrieved information is what is reflected in the relative slowing of RTs to these items relative to unstudied items. One possibility is that the information is in the form of a signal that supports familiarity in the absence of recollection. This possibility is buttressed by the consistently reported finding that familiarity-based recognition is associated with enhanced activity in the vicinity of the intraparietal sulcus (see Kim, 2011; Vilberg & Rugg, 2008b, for review), the region in this study where all four classes of studied item elicited reliable old/new effects. Along with the frontal nontarget effects discussed below, the findings of word task nontarget old/new effects in regions previously implicated in familiarity-based recognition, but not in regions sensitive to recollection, suggests that the gating of recollection by the adoption of a specific retrieval orientation does not extend to the retrieval of other sources of information about prior occurrence.

If nontarget recollection in the word task was gated, but these items nonetheless elicited a familiarity signal, on what basis were they rejected as nontargets? A likely possibility is that participants adopted the strategy originally proposed by Herron and Rugg (2003a) as a basis for nontarget rejection in an exclusion task. These authors (see also Herron & Wilding, 2005; Herron & Rugg, 2003b; Jacoby et al., 1999) argued that the adoption of a retrieval orientation that prevents the recollection of nontarget information allows targets to be identified merely by detecting the occurrence of recollection, obviating the need to evaluate the content of what was recollected. Conversely, any item for which recollection is unsuccessful can be rejected as a nontarget. We conjecture that in the present case (and in the studies of Johnson & Rugg, 2006; Herron & Rugg, 2003a) participants relied upon this strategy in the word task (but not, of course, the picture task, when recollection was not gated). We further conjecture that detection of the relatively high familiarity of the word task nontargets caused participants to delay responding while checking that this evidence of past occurrence was unaccompanied by a recollection signal. Consistent with evidence implicating left opercular and medial frontal cortex in control of retrieval (Ranganath, Heller, & Wilding, 2007; Gilboa et al., 2006; Simons, Owen, Fletcher, & Burgess, 2005; Dobbins, Rice, Wagner, & Schacter, 2003; Moscovitch, 1992), the nontarget old/new effects evident in these regions (Figure 2) may reflect engagement of postretrieval processes supporting evaluation of the information retrieved in response to these items (presumably, a combination of recollection- and familiarity-based information in the picture task and familiarity only in the word task; see also Yonelinas, Otten, Shaw, & Rugg, 2005).

## Conclusions

The present data provide strong converging evidence that the adoption of a retrieval orientation can gate the retrieval of goal-irrelevant information and prevent its recollection, supporting and extending previous ERP and fMRI findings. As predicted, nontarget old/new effects in left inferior parietal cortex varied with retrieval orientation, consistent with other evidence that this region has a specific role in recollection. This finding corresponds closely with the pattern previously observed for left parietal ERP old/new effects, converging with other data that suggest a common set of neural generators for these ERP and fMRI effects. Additionally, the present findings go beyond those of prior ERP studies to demonstrate that even when recollection is gated, studied items that are incongruent with targeted memory representations are nonetheless identified as familiar. Thus, the basis for the rejection of nontarget items depends upon the retrieval orientation adopted. Together, the findings help to build a more complete picture of the cognitive operations engaged in the control of memory retrieval and their neural bases.

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## REFERENCES

- Anderson, M. C., & Bjork, R. A. (1994). Mechanisms of inhibition in long-term memory: A new taxonomy. In D. Dagenbach & T. H. Carr (Eds.), *Inhibitory processing in attention, memory and language* (pp. 265–325). San Diego, California: Academic Press.
- Andersson, J. L. R., Hutton, C., Ashburner, J., Turner, R., & Friston, K. (2001). Modeling geometric deformations in EPI time series. *Neuroimage*, *13*, 903–919.
- Andrade, A., Paradis, A.-L., Rouquette, S., & Poline, J.-B. (1999). Ambiguous results in functional neuroimaging data analysis due to covariate correlation. *Neuroimage*, *10*, 483–486.
- Ashburner, J., & Friston, K. J. (2000). Voxel-based morphometry-The methods. *Neuroimage*, *11*, 805–821.
- Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues*. Leipzig: Barth.
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*, *9*, 613–625.
- Cocosco, C. A., Kollokian, V., Kwan, R. K. S., & Evans, A. C. (1997). Brainweb: Online interface to a 3D MRI simulated brain database. *Neuroimage*, *5*, 425.



- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, 29, 162–173.
- Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory & Cognition*, 28, 923–938.
- Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia*, 41, 318–333.
- Dywan, J., Segalowitz, S. J., & Webster, L. (1998). Source monitoring: ERP evidence for greater reactivity to nontarget information in older adults. *Brain and Cognition*, 36, 390–430.
- Dzulkifli, M. A., Herron, J. E., & Wilding, E. L. (2006). Memory retrieval processing: Neural indices of processes supporting episodic retrieval. *Neuropsychologia*, 44, 1120–1130.
- Dzulkifli, M. A., Sharpe, H. L., & Wilding, E. L. (2004). Separating item-related electrophysiological indices of retrieval effort and retrieval orientation. *Brain and Cognition*, 55, 433–443.
- Dzulkifli, M. A., & Wilding, E. L. (2005). Electrophysiological indices of strategic episodic retrieval processing. *Neuropsychologia*, 43, 1152–1162.
- Friston, K. J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *Neuroimage*, 7, 30–40.
- Friston, K. J., Glaser, D. E., Henson, R. N., Kiebel, S., Phillips, C., & Ashburner, J. (2002). Classical and Bayesian inference in neuroimaging: Applications. *Neuroimage*, 16, 484–512.
- Gilboa, A., Alain, C., Stuss, D. T., Melo, B., Miller, S., & Moscovitch, M. (2006). Mechanisms of spontaneous confabulations: A strategic retrieval account. *Brain*, 129, 1399–1414.
- Goh, W. D., & Lu, S. H. X. (2012). Testing the myth of the encoding-retrieval match. *Memory & Cognition*, 40, 28–39.
- Guerin, S. A., & Miller, M. B. (2011). Parietal cortex tracks the amount of information retrieved even when it is not the basis of a memory decision. *Neuroimage*, 55, 801–807.
- Henson, R., Andersson, J., & Friston, K. (2000). Multivariate SPM: Application to basis function characterisations of event-related fMRI responses. *Neuroimage*, 11, 468.
- Herron, J. E., & Rugg, M. D. (2003a). Retrieval orientation and the control of recollection. *Journal of Cognitive Neuroscience*, 15, 843–854.
- Herron, J. E., & Rugg, M. D. (2003b). Strategic influences on recollection in the exclusion task: Electrophysiological evidence. *Psychonomic Bulletin & Review*, 10, 703–710.
- Herron, J. E., & Wilding, E. L. (2005). An electrophysiological investigation of factors facilitating strategic recollection. *Journal of Cognitive Neuroscience*, 17, 777–787.
- Hornberger, M., Morcom, A. M., & Rugg, M. D. (2004). Neural correlates of retrieval orientation: Effects of study–test similarity. *Journal of Cognitive Neuroscience*, 16, 1196–1210.
- Hornberger, M., Rugg, M. D., & Henson, R. N. (2006a). fMRI correlates of retrieval orientation. *Neuropsychologia*, 44, 1425–1436.
- Hornberger, M., Rugg, M. D., & Henson, R. N. A. (2006b). ERP correlates of retrieval orientation: Direct versus indirect memory tasks. *Brain Research*, 1071, 124–136.
- Jacoby, L. L., Kelley, C. M., & McElree, B. D. (1999). The role of cognitive control: Early selection versus late correction. In S. Chaiken & Y. Trope (Eds.), *Dual-process theories in social psychology* (pp. 383–400). New York: Guilford Press.
- Jacoby, L. L., Shimizu, Y., Daniels, K. A., & Rhodes, M. G. (2005). Modes of cognitive control in recognition and source memory: Depth of retrieval. *Psychonomic Bulletin & Review*, 12, 852–857.
- Johnson, J. D., & Rugg, M. D. (2006). Modulation of the electrophysiological correlates of retrieval cue processing by the specificity of task demands. *Brain Research*, 1071, 153–164.
- Johnson, M. K., Kounios, J., & Nold, S. F. (1997). Electrophysiological brain activity and memory source monitoring. *NeuroReport*, 8, 1317–1320.
- Kim, H. (2011). Differential neural activity in the recognition of old versus new events: An activation likelihood estimation meta-analysis. *Human Brain Mapping*. doi: 10.1002/hbm.21474.
- Madigan, S. (1983). Picture memory. In J. C. Yuille (Ed.), *Imagery, memory and cognition: Essays in honor of Allan Paivio* (pp. 65–89). Hillsdale, NJ: Erlbaum.
- Mecklinger, A. (2010). The control of long-term memory: Brain systems and cognitive processes. *Neuroscience and Biobehavioral Reviews*, 34, 1055–1065. doi: 10.1016/j.neubiorev.2009.11.020.
- McDuff, S. G., Frankel, H. C., & Norman, K. A. (2009). Multivoxel pattern analysis reveals increased memory targeting and reduced use of retrieved details during single-agenda source monitoring. *Journal of Neuroscience*, 29, 508–516.
- Mintzer, M. Z., & Snodgrass, J. G. (1999). The picture superiority effect: Support for the distinctiveness model. *American Journal of Psychology*, 112, 113–146.
- Morcom, A. M., & Rugg, M. D. (2004). Effects of age on retrieval cue processing as revealed by ERPs. *Neuropsychologia*, 42, 1525–1542.
- Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior*, 16, 519–533.
- Moscovitch, M. (1992). Memory and working-with-memory—A component process model based on modules and central systems. *Journal of Cognitive Neuroscience*, 4, 257–267.
- Nairne, J. S. (2002). The myth of the encoding-retrieval match. *Memory*, 10, 389–395.
- Penny, W., & Holmes, A. (2006). Random effects analysis. In K. Friston, J. Ashburner, S. Kiebel, T. Nichols, & W. Penny (Eds.), *Statistical parametric mapping: The analysis of functional brain images* (pp. 156–165). London: Elsevier.
- Ranganath, C., Heller, A. S., & Wilding, E. L. (2007). Dissociable correlates of two classes of retrieval processing in prefrontal cortex. *Neuroimage*, 35, 1663–1673.
- Ranganath, C., & Paller, K. A. (1999). Frontal brain potentials during recognition are modulated by requirements to retrieve perceptual detail. *Neuron*, 22, 605–613.
- Robb, W. G., & Rugg, M. D. (2002). Electrophysiological dissociation of retrieval orientation and retrieval effort. *Psychonomic Bulletin & Review*, 9, 583–589.
- Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, 11, 251–257.
- Rugg, M. D., Johnson, J. D., Park, H., & Uncapher, M. R. (2008). Encoding-retrieval overlap in human episodic memory: A functional neuroimaging perspective. *Progress in Brain Research*, 169, 339–352.
- Rugg, M. D., Mark, R. E., Walla, P., Schloerscheidt, A. M., Birch, C. S., & Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory. *Nature*, 392, 595–598.
- Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Sciences*, 4, 108–115.
- Schacter, D. L., Buckner, R. L., Koutstaal, W., Dale, A. M., & Rosen, B. R. (1997). Late onset of anterior prefrontal activity during true and false recognition: An event-related fMRI study. *Neuroimage*, 6, 259–269.
- Simons, J. S., Owen, A. M., Fletcher, P. C., & Burgess, P. W. (2005). Anterior prefrontal cortex and the recollection

- of contextual information. *Neuropsychologia*, 43, 1774–1783.
- Skinner, E. I., & Fernandes, M. A. (2007). Neural correlates of recollection and familiarity: A review of neuroimaging and patient data. *Neuropsychologia*, 45, 2163–2179.
- Stenberg, G., Johansson, M., & Rosen, I. (2006). Conceptual and perceptual memory: Retrieval orientations reflected in event-related potentials. *Acta Psychologica (Amst)*, 122, 174–205.
- Stenberg, G., Radeborg, K., & Hedman, L. R. (1995). The picture superiority effect in a cross-modality recognition task. *Memory & Cognition*, 23, 425–441.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: George Thieme Verlag.
- Tulving, E., & Osler, A. (1968). Effectiveness of retrieval cues in memory for words. *Journal of Experimental Psychology*, 77, 593–601.
- Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, 80, 353–373.
- Vilberg, K. L., Moosavi, R. F., & Rugg, M. D. (2006). The relationship between electrophysiological correlates of recollection and amount of information retrieved. *Brain Research*, 1122, 161–170.
- Vilberg, K. L., & Rugg, M. D. (2007). Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia*, 45, 2216–2225.
- Vilberg, K. L., & Rugg, M. D. (2008a). Functional significance of retrieval-related activity in lateral parietal cortex: Evidence from fMRI and ERPs. *Human Brain Mapping*, 30, 1490–1501.
- Vilberg, K. L., & Rugg, M. D. (2008b). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, 46, 1787–1799.
- Vilberg, K. L., & Rugg, M. (2009). Lateral parietal cortex is modulated by amount of recollected verbal information. *NeuroReport*, 20, 1295–1299.
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9, 445–453.
- Woodruff, C. C., Uncapher, M. R., & Rugg, M. D. (2006). Neural correlates of differential retrieval orientation: Sustained and item-related components. *Neuropsychologia*, 44, 3000–3010.
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience*, 25, 3002–3008.